Transactions of the Royal Society of S. Aust. (1996), **120**(3), 83-99.

THE BREEDING BIOLOGY OF *LITORIA SUBGLANDULOSA* AND *L. CITROPA* (ANURA: HYLIDAE), AND A RE-EVALUATION OF THEIR GEOGRAPHIC DISTRIBUTION

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Summary

ANSTIS, M. & LITTLEJOHN, M. J. (1996) The breeding biology of *Litoria subglandulosa* and *L. citropa* (Anura: Hylidae), and a re-evaluation of their geographic distribution. *Trans. R. Soc. S. Aust.* **120**(3), 83-99, 29 November, 1996.

The known range of *Litoria subglandulosa* is extended and that of *L. citropa* is revised. Population trends observed at the type locality during the 1960s-70s and 1990s are compared.

The advertisement call, adult colouration in life, behaviour and embryological development of *L. subglandulosa* are described and compared with those of *L. citropa*. The single egg mass of *L. subglandulosa* shows adaptation to the lotic environment, being compact and strongly adherent. The embryos and larval stages of the two species are very similar in shape and colour in life from stage 17 onwards, but are readily distinguishable by mouthparts. Comparative notes on larval behaviour are given.

KEY WORDS: *Litoria subglandulosa, Litoria citropa,* distribution, population trends, advertisement calls, oviposition, embryology, larval behaviour.

Introduction

Litoria subglandulosa was described as *Litoria glandulosa* Tyler & Anstis, 1975 but renamed because of primary homonymy (Tyler & Anstis, 1983). A member of the *L. citropa* species group (Tyler & Davies 1978), *L. subglandulosa* was previously known only from the Queensland/NSW border south to the New England ranges of northern NSW (Tyler & Anstis 1975). The type description included a description of the larvae, but no data were available on oviposition, embryological development, larval behaviour or the advertisement call.

The species was found 160 km south of its previous known distribution in the mid-north coastal ranges and Barrington Tops region by one of us (M.A.), in 1977. Its presence there and the absence of *L. citropa*, prompted a re-examination of the distribution of both species. In addition, observations on oviposition, the morphology of embryos, larvae and adults and a comparison of the advertisement calls of *L. citropa* and *L. subglandulosa* were made and are reported here.

Materials and Methods

Litoria subglandulosa

Adult specimens examined: Australian Museum (AM) R17577, 35525, 42934-35, 50163, 51096-7, 51104, 5173549, Point Lookout; R34458 - 14km East of Ebor; R36724 - Oakey Creek near Ebor; R36975 - Guy Fawkes River, Ebor; R71109-71114 - Back Creek (Barwick River) near Point Lookout; R37017 - 5km S of Walcha ; R39056 - 50km E of Glen Innes (Gibraltar Range); R52931 - Sandys Creek, Dorrigo; R51178-80 – Styx River, Point Lookout; R76519 - Gloucester Tops; R31683 – Upper Allyn River, Barrington Tops; R104932 – Ellenborough River, Bulga State Forest, NSW.

Litoria citropa

Adult specimens examined: Australian Museum R7560, Orbost; 7562, Aberfeldy, Vic.; 19237, 18234, 18236, 18238 Stanwell Tops; 79436, Stanwell Park; 24500-24505, 27590, Faulconbridge; 45858, Thirlmere Lakes; 31685, 7112, 78927 Helensburgh; 45424, Tianjara Falls; 5188, Megalong Valley; 7110, Hazelbrook; 5008, Blackheath; 69034, Bell, Kurrajong Rd.; 76625, 18 km N of Lithgow; 8459, Pennant Hills; 14495, Colo Vale; 79100, 76623, Culoul Range N of Colo Hts.; 4261, Bundanoon; 71898, 24 km N of Moss Vale; 15462, Gosford; 78264-26, 78698, Kuringai-Chase; 60425, Nadgee Reserve; 79439, Galston Gorge; 7563, Manly, NSW.

Three adults cited as *L. citropa* by Tyler & Anstis (1975) from Barrington Tops localities:- Dept Zool., Univ. Melbourne (MUZD) 1792/64 - Upper Allyn and MUZD 1690-91/63 - Wombat Creek, were re-examined because of apparent overlap in range with the Barrington Tops localities for *L. subglandulosa*. These specimens have since been registered by the National Museum of Victoria (NMV) as D32666 (Upper Allyn River) and D32664-65 (Wombat Creek). Similarly, two specimens (NMV D6709-10), cited by Copland (1957) as *L. citropa* from near Grafton, north-eastern NSW, were examined.

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TABLE 1. *Details of localities, habitats and field observations for* Litoria subglandulosa.

No.	Locality	Alt.(m)	Habitat/Weather	Date/Time	Adults Calling	Temp. (dry, bulb; dry/wet/ water °C)	Larval Stages (*L.sub.*)	Larvae of Other Species Present
1	9.8 km E. of Elands NSW 31° 36′59″S 152° 24′00″E	680	Permanent flowing stream, basalt/sand.	19.i.1977 2010 h	-	-	25-42	*Mixophyes balbus* *M. fasciolatus*
			Semi-cleared wet sclerophyll forest.	20.i.1977 1100 h	-	-	25-42	*L. pearsoniana*
				16.i.1996 1020 h	-	20/19.5/16	Nil	*Crinia signifera* *L. pearsoniana*
2	Tirrill Creek, Bulga State Forest NSW 31° 31′49″S 152° 08′21″E	520	Permanent flowing stream, metamorphic/sand. Rainforest, overhead canopy.	28.xii.1979 - 2.x. 1980 am/pm	Diurnal calling 3+ ♂♂	-	26-46 (many at stage 46	*M. balbus* *L. pearsoniana*
			Light rain, overcast after good rain on 3.x.1980	4.x.1980 1800-1930 h	6 ♂♂	16 -17	No search	No search
				7.xii.1980 1545 h	1 gravid ♀	-	30-42	*M. balbus*
				8.xii.1980 pm	1 ♂	15/14.75	30-42	*L. pearsoniana*
				9.xii.1980 0720 h	-	Water 15	30-42	*M. balbus* *L. pearsoniana*
			Overcast, light rain after long dry period of over 6 months.	20.i.1994 am pm	- 1 ♂	22 19.5/18.5	40-44 (6 only)	*L. phyllochroa* *M. balbus*
			Warm, sunny, rain previous week	16.i.1996 1400 h	-	27/24/19	39-42 (7 only)	*L. lesueuri* *L. pearsoniana*
3	Ellenborough River Bulga State Forest NSW 31° 35′31″S 152° 12′09″E	610	Permanent flowing stream, basalt/sand.	1.i.1980 pm	-	-	32-38	*M. balbus*
			Wet sclerophyll forest.	5.x.1980 pm 6.x.1980 1300 h	8 ♂♂ 1 gravid ♀	-	Nil	*M. balbus*
4a	Frenchs Creek Bulga State Forest NSW 31° 33′35″S 152° 11′27″E	580	Permanent flowing creek, metamorphic/sand. Wet sclerophyll forest.	7.xii.1980 1915 h	3 ♂♂	16/15.5	No search	*M. fasciolatus* *L. pearsoniana* *L. phyllochroa*
4b	As above 31° 33′40″S 152° 12′26″E	520	As above	7.xi.1980 1945 h	2 ♂♂	16/15.5	"	As above
				8.xii.1980 pm	1 ♂	15		
				20.i.1994 pm	-	22	Nil	Nil
				16.i.1996 1600 h	-	23/20/18.5	28, 37 (2 only)	*L. pearsoniana*

TABLE 1. *Continued.*

5a	Dilgry Creek Barrington Tops NSW 31° 59′ 19″ S 151° 33′ 28″ E	1180	Permanent flowing small creek, basalt/sand Wet sclerophyll forest. Hot, dry day, brief storm.	25.xii.1979 1400 h	-	-	26-41	*M. balbus* *C. signifera*
5b	Dilgry River Barrington Tops NSW	1160	Permanent flowing stream, basalt/sand.	25.xii.1979 1430 h	-	-	26-41	*C. signifera*
	As above 31° 53′ 23″ S 151° 32′ 17″ E		Wet sclerophyll forest. *Eucalyptus*, *Casuarina*, *Acacia*, *Leptospermum*	26.xii.1979 pm	1 ♂	-	-	
				20.x.1994 am	groups of 3 ♂♂ undercover	23	-	
				20.x.1994 1900 h	40 ♂♂ in 3 groups of up to 6	9.8 Water 13.4	-	
6a	Polblue Creek Barrington Tops NSW 31° 53′ 18″ S 151° 25′ 57″ E	1450	Permanent flowing creek, basalt. Montane swampland. *Eucalyptus pauciflora*, *Danthonia* (tussock grass)	26.xii.1979 1400 h	-	-	26-43	*M. balbus* *C. signifera*
6b	As above 31° 55′ 38″ S 151° 23′ 14″ E	1230	Permanent flowing creek, basalt. Montane forest.	19-20.xii.1994 pm	6 ♂♂	-	No search	-
7a	Manning River Barrington Tops NSW 31° 52′ 53″ S 151° 29′ 21″ E	1190	Permanent river, wet sclerophyll forest	26.xii.1979 pm	-	-	26-43	*M. balbus* *C. signifera*
7b	As above 31° 52′ 52″ S 151° 29′ 34″ E	1220	As above. Clear sky, gusty winds	6.xi.1994 2030 - 2121 h	5 ♂♂	15 Water 13.5	-	-
			Very strong winds	7.xi.1994 0742 h	4 ♂♂	-	-	-
8	Tuckers Creek Barrington Tops NSW 31° 51′ 58″ S 151° 39′ 12″ E	750	Permanent stream, basalt, Wet sclerophyll forest	4.xi.1994 1400 h	2 ♂♂	16.8 Water 9.4	8 egg masses	*M. balbus* *C. signifera*
9	Fal Brook Mount Royal State Forest Barrington Tops NSW 32° 09′ 42″ S 151° 18′ 46″ E	750	Permanent stream, wet sclerophyll forest.	8.xi.1992	1 ♂	-	No search	No search

TABLE 1. *Continued.*

No.	Locality	Alt.(m)	Habitat/Weather	Date/Time	Adults Calling	Temp. (dry, bulb; dry/wet/ water °C)	Larval Stages (*L.sub.*)	Larvae of Other Species Present
10	Back Creek (Barwick River) Point Lookout NSW 30° 29′29″S 152° 20′38″E	1340	Permanent stream, basalt/sand, partly cleared grazing land. Montane wet sclerophyll forest	1.i.1972 1415 h	2 ♂♂, 7 juveniles	22 Water 23	25-46	*M. balbus* *C. signifera*
				29-30.xii.1973 am/pm	10 + ♂♂ 2 gravid ♀♀	-	25-46	*L. booroolongensis* *L. pearsoniana*
				5.i.1974 2115 h	2 ♂♂	15.5-14	25-46	As above
				19.xii.1994 1700 h	Nil	-	Nil	None present
11	Styx River Point Lookout NSW 30° 30′34″S 152° 21′56″E	1320	Permanent river, basalt/sand, partly cleared grazing land. Montane wet sclerophyll forest.	26.xii.1973 am	-	- Water 15	25-43	*M. balbus* *C. signifera* *L. pearsoniana* *L. booroolongensis*
				19.xii.1994 1720 h	-	-	Nil	None present
12	Mobong Creek Wild Cattle Creek State Forest NE Dorrigo NSW 30° 10′29″S 152° 53′48″E	510	Permanent stream, basalt/sand. Wet sclerophyll forest. *Eucalyptus*, *Ceratopetalum*, *Acacia.*	19.xii.1994 1500 h	-	25.5/18/24	25-27	*M. iteratus.* *M. balbus* *L. pearsoniana* *L. booroolongensis* *L. chloris*
13a	Upper reaches Diehard Creek 32km E Glen Innes NSW 29° 40′04″S 152° 03′25″E	980	Permanent small creek, granite/quartz/sand. Dry sclerophyll forest. *Eucalyptus*, *Acacia*, *Pteridium*, *Blechnum* ferns.	20.x.1993 2200 h	1 ♂ (recorded)	13	No search	No search
13b	As above 29° 40′12″S 152° 03′38″E	940	As above. Warm, sunny day.	20.xii.1994 1400 h	-	34 Water 22	27-32	Nil
14	Coombadjha Creek, Washpool Nat. Park NE Glen Innes NSW 29° 28′24″S 152° 19′11″E	770	Permanent river, granite, quartz, gravel, sand. Rainforest. *Ceratopetalum*, *Eucalyptus*, *Acacia*, *Acmena*, *Quintinia*, *Cyathea*, *Todea* etc. Warm, sunny day.	21.xii.1994 1400 h	-	28 Water 22	36-43	*M. balbus* *L. pearsoniana*

TABLE 2. *Observations on adult behaviour in relation to oviposition* - Litoria subglandulosa

Locality No. (See Table 1)	Date/Time	Weather	Temp. (dry bulb: dry/ wet bulb. °C)	Surface Water Temp °C	Adult Activity/Site of Collection	Oviposition Site	No. of Eggs
10	30-31.xii.1973 am/pm	Clear Sky	15	-	Nocturnal: 7 ♂♂ calling beside stream. Diurnal: Gravid ♀ beside stream 2m from calling ♂. Calling in bag prior to amplexus		
	1.i.1974 0100-0930		-	16	Oviposition	In plastic bag attached below surface	292
3	5.x.1980 pm	Clear sky. Rain previous night	16-17	8	8 ♂♂ calling		
	6.x.1980 1300	Clear, sunny	19	-	Gravid ♀ on log just above streamside in daylight. Calling ♂ collected here previous night		
	6.x.1980 0300-0900	As above	-	-	Oviposition	In plastic bag	425
2	7.xii.1980	Clear, sunny	-	-	Gravid ♀ on rock just above streamside	-	-
4a	7.xii.1980 2145	Clear sky	16.5/15.5	-	2 ♂♂ calling on branch 3m above water. 1 collected	-	-
4b	7-8.xii.1980 2200-0900		-	-	Oviposition - ♀ from loc. 2, ♂ from loc. 4	In plastic bag	-
5b	20.x.1994 0630	Warm, clear, no rain previous nights	8.5	9.3	Diurnal: ♂♂ calling undercover in groups of up to 3, along 150 m section of stream.	-	-
	1900	Some night fogs	9.8	13.4	Nocturnal: 40 ♂♂ calling from branches. vegetation beside stream in groups of up to 6	-	
8	4.xi.1994 1130	Rain previous few days	16.8	9.4	2 ♂♂ calling	8 egg masses, each attached just below surface to leaf, twig, rock in flowing water of pools	-

TABLE 3. *Observations on adult behaviour in relation to oviposition* - Litoria citropa

No.	Locality	Alt. (m)	Date/Time	Weather/Temp.(dry bulb, °C)	Adult Activity	Oviposition Site	No. of Eggs
15	Maddens Creek Darkes Forest NSW 34° 13′02″S 151° 00′00″E	350	30.x.1972	Overcast night after one week of rain. 17	1 gravid ♀ collected on road 50m from stream.	-	-
	As above		2.xi.1972	Overcast night after rain. 17	4 ♂♂ calling beside stream. 1 ♂ placed in plastic bag with ♀. Amplexus, but no eggs.	-	-
	As above		6.xi.1972	Overcast night after storm. 19.5	3 ♂♂ calling, 1 gravid ♀ beside stream. 1 ♂ placed with ♀ in bag. Oviposition	Eggs scattered over bottom of bag.	890
	As above		16.ix.1975	Overcast night light rain. 18	10 ♂♂ calling 2 gravid ♀♀. 1 ♂ placed in bag with 1 ♀. Oviposition	Scattered over floor of large dish of water in cage.	928
16	Ourimbah Creek Ourimbah NSW 33° 19′09″S 151° 17′53″E	50	25.xi.1973	Dry, warm, partly overcast night	1 ♂, 1 gravid ♀ sitting near each other beside stream. Placed in bag. Oviposition	Scattered over bottom of bag	655

Oviposition and embryos

Observations on three captive breeding pairs of each species, collected by M.A., are summarised in Tables 2 and 3. In each case, a calling male was first collected at night, then a gravid female was found during daylight the next day, in the same vicinity as the male. The pairs were each placed in a large inflated plastic bag containing stream water, a flat rock and aquatic vegetation. The bag was covered with opaque material for the duration of amplexus.

Litoria subglandulosa

Stages 1-25 (Gosner, 1960) were studied from three separate egg masses, one from the type locality (locality 10, Table 1), and the others from the new localities 3 and 4b. Hereafter, numbered localities will refer to Table 1 (unless otherwise stated). Further samples from egg masses found in the stream at locality 8 were maintained until stage 25 to confirm identity, by Dr A. White of the National Parks & Wildlife Service, NSW (NP&WS). Embryos and larvae were held in dishes (40 cm diam.) containing stream water, rocks, sediments and aquatic vegetation, and maintained at 14°-21°C (locality 9), and 15°-24°C (localities 3 and 4b).

The egg mass from locality 4b laid on 7.xii.1980 (Table 2), was submerged within a metal tea strainer in the cool, flowing water of the stream for the initial two days of development, but both the egg masses from localities 3 and 4b were maintained at higher temperatures of up to 24°C away from the stream from the third day after deposition. Embryonic development was observed under a Wild M5 stereoscopic microscope.

Litoria citropa

Stages 1 - 25 were studied from two egg masses from Darkes Forest and one from Ourimbah (localities 15 & 16, Table 3). Samples of eggs found scattered over the substrate in the stream were raised to stage 25 to confirm identity. Adults in breeding condition were placed in an inflated plastic bag covered with opaque material during amplexus and the resulting embryos maintained at 16°-23°C.

Larvae

Tadpoles were measured (to 0.1 mm) with vernier callipers and an ocular micrometer attached to the microscope. They were anaesthetised in Chlorbutol solution before preservation in 3% formalin. The staging system is that of Gosner (1960). Abbreviations for larval measurements shown in Table 6, follow Anstis (1976): TL = total length, BL = body length, BD = maximum body depth, TD = maximum tail depth, TM = tail musculature depth (measured in line with TD), IO = interorbital span, IN = internarial span, EN = the distance between eye and naris and MW = maximum mouth width. Illustrations were made using a drawing tube attached to the microscope. Preserved and living larvae of *L. subglandulosa* from sites 1 - 9 were examined for comparison with those from the type locality and measurements are given in Table 6. Feeding and swimming behaviour of several larvae of both species was observed in captivity and in their natural lotic environment.

Advertisement calls

The calls of *L. subglandulosa* were recorded at a tape speed of 4.76 cm sec^{-1}, using a Sony TC-D5PRO portable cassette recorder with a Uher M516 microphone and a Grampian parabolic reflector. Calls of *L. citropa* were recorded with a Nagra 4.2 open-reel tape recorder at a tape speed of 19 cm sec^{-1}, and a Beyer M-88 cardioid dynamic microphone.

For *L. subglandulosa*, the tape cassette was replayed on a Nakamichi Dragon tape deck, and for *L. citropa*, the open-reel tape was replayed on either a Revox B-77 or a Sony TC-510-2 tape recorder. The calls were analysed on a Kay Elemetrics Digital Sona-Graph, Model DSP-5500. Additional analyses of waveforms were made by way of a Sound-Blaster 16 card (Creative Technology) installed in an IBM PC-compatible desktop computer, and using the Wave Studio (Creative Technology) and Spectra Plus Professional, Release 3.0 (Pioneer Hill) software. Both systems yielded consistent results for analysis of the same signals.

The dominant (= peak) frequencies were calculated as those of greatest amplitude in a power spectrum or an averaged spectral display. Numbers of pulses were determined by inspection of waveforms. Pulse rates were calculated from the interval between the peak of the first pulse and the peak of the last pulse in a pulse train and the number of pulses reduced by one (i.e., n-1 pulses). Because of the difficulty in determining the beginnings and ends (i.e., zero amplitudes) of pulses and pulse trains, the peak - peak interval was taken as the duration. Where appropriate, pulse trains are termed 'notes'. If two distinctly different types of temporal unit are present in a call, then the signal is described as diphasic (*sensu* Littlejohn & Harrison 1985).

Results

Distribution and habitat

Litoria subglandulosa

The new localities (1-9) recorded in Table 1 extend the known southern range of this species about 180 km. All localities are permanent streams/rivers of basalt or metamorphic rock country associated with rainforest, montane or wet sclerophyll forest (except for 13a & 13b) and are at 510 m or higher. The

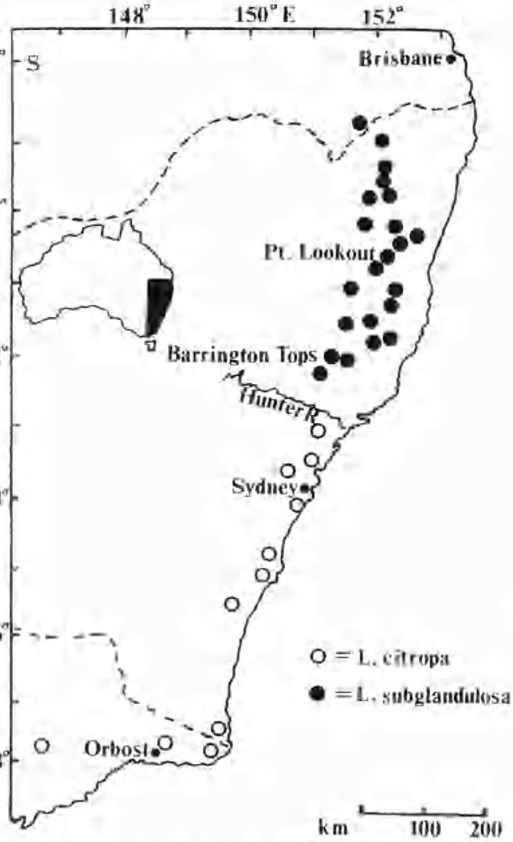


Fig. 1. A revision of the distribution of *Litoria citropa* and *Litoria subglandulosa* provided by Tyler & Anstis (1975), including a number of new localities for *L. subglandulosa*.

southernmost locality at which the species has been found is locality 9, Fal Brook, Mount Royal State Forest, NSW. The National Parks & Wildlife North-east Forests Biodiversity Study (1991-1994) records *L. subglandulosa* at a number of sites between the Barrington Tops region and the northernmost forests of NSW, including Doyles River State Forest, Mt Boss State Forest, Nowendoc, Werrikimbe National Park, Gibraltar Range National Park, Styx State Forest, Spirabo State Forest and Boonoo State Forest. This indicates the species has a fairly continuous distribution along the range country, from locality 9 in the south to near Stanthorpe, just north of the Qld/NSW border (151° 40'30"E, 28° 40'20"S) (Fig. 1).

On a daytime visit to localities 10 and 11 on 19.xii.1994, no tadpoles of this or other species were located. This was at a time when numerous tadpoles of *L. subglandulosa*, *L. booroolongensis* and *Mixophyes balbus* would be expected to be present (based on annual studies in the 1960s and '70s). Observations by John de Bavay and Paul Webber confirm that there has been little evidence of this frog over recent years at the type locality, suggesting that the species may be undergoing a decline there. The National Parks and Wildlife Biodiversity Study has records of five males of this species calling at three sites on 2.ix.1995 in the Styx River State Forest in the region of the type locality:

1) Eely Creek - lat./long. 30° 34'39"E, 152° 14'43"S, (altitude 1060 m)
2) Eely Creek - 30° 35'26"E, 152° 13'18"S, (890 m)
3) Wattle Flat Camping Area - 30° 35'28"E, 152° 12'38"S (870m).

Observations on 20.xii.1994 at localities 12, 13b and 14 (all northern localities), indicated the presence of *L. subglandulosa* tadpoles.

Litoria citropa

Specimens NMV D32666 (Upper Allyn River) and D32664-65 (Wombat Creek) were examined and, on the basis of the indistinct tympanum, prominent supratympanic fold and head width, were found to be *L. subglandulosa*. NMV D6709-10 cited by Copland (1957) as *L. citropa* from near Grafton in the north-east coast of NSW, form the basis of the statement by Heatwole *et al.* (1995) that *L. citropa* "extends from northeastern New South Wales to southeastern Victoria". Upon examination, these specimens were found to have the body proportions of *L. subglandulosa*, but because both were collected in 1865 and in a poor state of preservation, it is difficult to come to a definite conclusion as to their identity. The two species have not been found in sympatry at any site examined, and this fact, in combination with the examination of museum material, indicates that the drainage of the Hunter River appears to be a natural geographic barrier separating them (Fig.1).

Larvae were observed by M.A. on 1.i.1976 and 25.i.1996 at Boardinghouse Dam in the Watagan State Forest, south of the Hunter river NSW (33° 00'01"E, 151° 24'15"S) and by R. Wells further north in the Pokolbin State Forest, near Cessnock, in January 1993. This is the northernmost known locality for this species.

Litoria subglandulosa appears to replace *L. citropa* in the Barrington Tops region north of Newcastle (Fig.1). *L. citropa* occupies a wider variety of habitats than *L. subglandulosa*, including permanent streams in basalt country associated with wet sclerophyll or montane forest, to similar streams in sandstone country. Although found at an altitude of 1066 m at Aberfeldy, Vic. and Blackheath, NSW, *L. citropa* also has been found in lower coastal areas to 50 m (locality 16, Table 3).

Adult colour in life

Litoria subglandulosa

Specimens from northern localities were predominantly green, whereas those from mid-north coastal localities (1 - 9) ranged from uniform golden brown with scattered darker mottling over the dorsum, to specimens with some small areas of green, often along the canthus rostralis or under the eye. Two males from locality 1 each had a broad dorsal patch of green over the head or dorso-lateral regions. Two specimens, AMR76519, from Gloucester Tops NSW, and another observed by H. Hines (NP&WS) at Fal Brook (locality 9), were uniform bright green, apart from the characteristic golden dorso-lateral stripes.

Some golden-brown specimens developed large bright green patches over the dorsum at night (S. Gow pers. comm.). The inner surfaces of the hind limb and groin area were translucent yellow, as found in adults from the type locality.

Litoria citropa

Litoria citropa has a uniform golden brown dorsal colouration (with green along the canthus rostralis and sides of the body), similar to most specimens of *L. subglandulosa* from localities 1-9. The principal difference between the species is the colour of the inner surfaces of the hind limb and groin, which in *L. citropa* is brick red.

Calling activity

Litoria subglandulosa

Calling begins in spring and was observed on 20.x.1994 at locality 8, when water temperatures at night were very low, e.g., 6°C, and the dry bulb air temperature at locality 5b (1900 h) was 9.8°C (A. White, S. Gow pers. comm.). Other observations by M.A. at the type locality during annual three-week periods (Dec./Jan. 1966-74), and at all other localities listed in Table 1, indicate that calling persists throughout December/January in a variety of weather conditions, with increased activity during, or after, light rain. Evening dry bulb air temperatures taken during periods of spring/summer activity at the localities in Table 1 were 13°C-19.5°C (mean 15.7°C). At the lower temperatures (13°-14°C), calling was less intense and by aural comparison only, notes were at a slower repetition rate.

Sporadic diurnal calling was common during the breeding season but males were most active at night. Diurnal calling took place from concealed positions such as under rocks or from within vegetation, either near the stream, or at times up to about four metres away from the water. A single male or a small number of individuals, called from as early as 0742 h (e.g., locality 7b). Nocturnal calling was initiated by one frog, normally followed by others in a distinctly polyphonic chorus. The calls of frogs at the southern localities could not be differentiated from those of males at the type locality.

Males observed calling at night were often perched on broad leaves of trees and shrubs approximately 0.5-1.5 m above streams, on ferns at the edge of the stream, or on vegetation further from the water's edge. They were frequently found calling in small groups, two or more metres apart. On 22.x.1994 at locality 5b, 40 males were calling at night in groups of up to six along a 50 m stretch of the stream (S. Gow pers. comm.). At locality 7b on 7.xi.1994, four males were calling 25 m apart (K. Thumm pers. comm.).

An analysis of the advertisement call is provided below and comparison made with that of *L. citropa*. Two additional call sequences, attributable to *L. subglandulosa*, are in the Bioacoustic Library of the Department of Zoology, University of Melbourne, both recorded by M. J. Littlejohn and his associates. The first, from Guy Fawkes Creek Ebor NSW (30° 24′ 20″ E, 152° 20′ 46″ S), was recorded on 28.x.1964 at a wet bulb air temperature of 8.5°C, and the second, from Flat Rock Creek 8 km W of Point Lookout NSW (close to the first site), on 14.x.1968 at a wet bulb air temperature of 13°C. They are similar in all pertinent respects to the call described here.

Litoria citropa

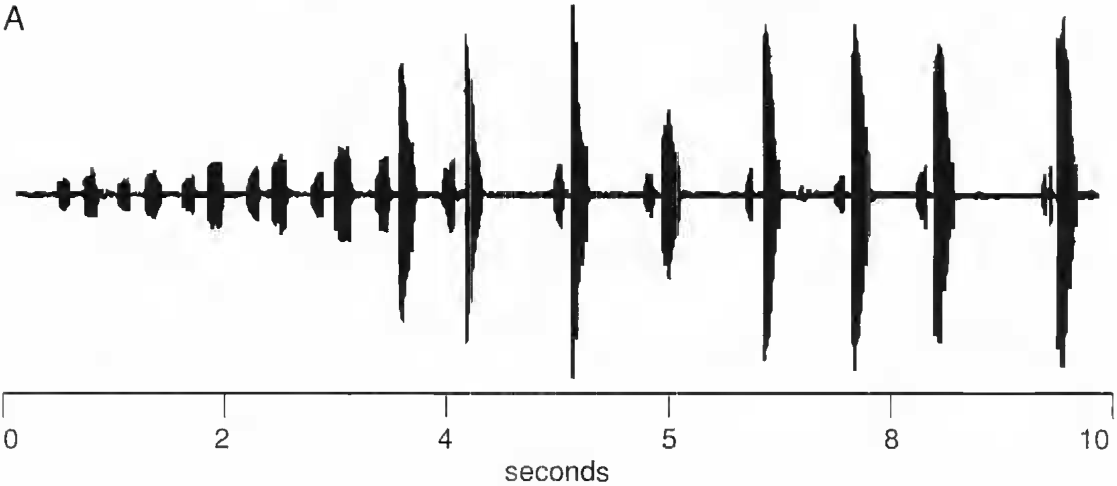
Males at Darkes Forest (locality 15, Table 3) were observed during spring and summer calling from low branches beside the stream, on rocks near the edge of the water, or on exposed rock shelf in mid-stream close to shallow, slowly flowing water. As with *L. subglandulosa*, males called while two or more metres apart and activity increased on overcast evenings during or after rain. Dry-bulb air temperatures on several nights when males were calling in September – December, 1972-1980, were 14°-22°C. No diurnal calling was observed.

Advertisement calls

Litoria subglandulosa

The advertisement call of *L. subglandulosa* was recorded by J. Courtney at Diehard Creek, Glen Innes (locality 13a), on 20.x.93. The dry-bulb air temperature was 13°C. The following data were obtained from the fourth call in the sequence (Fig. 3A). The call has a duration of 9.375 s and consists of 13 pairs (doublets) of pulse trains (notes), with each of those in the first five pairs all being of relatively low amplitude (Fig. 3b). In the subsequent seven pairs of notes, the second note is of much greater amplitude than the first. Thus, all but one of the first notes (which is of equal amplitude) are softer, with the amplitude of second notes being

Fig. 2. Live egg mass of *Litoria subglandulosa* attached to a leaf from submerged overhanging foliage in Tuckers Creek, Barrington Tops (locality 8). Scale bar = 10mm.



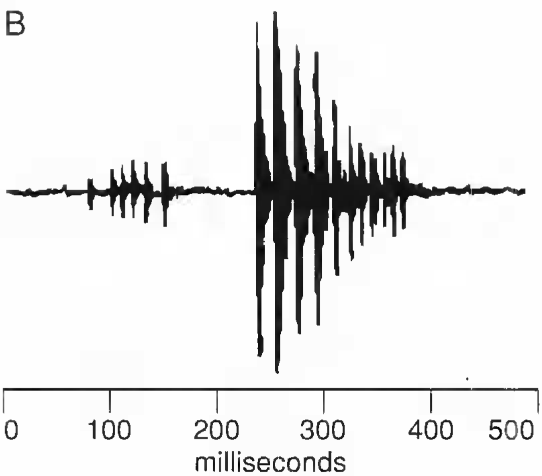
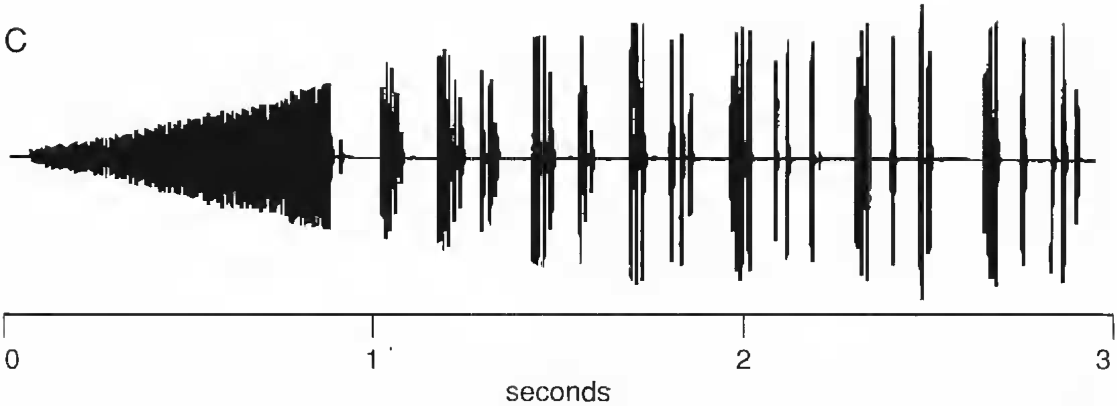


Fig. 3. Waveforms of advertisement calls of *Litoria subglandulosa* and *L. citropa*.
A. The complete advertisement call of *Litoria subglandulosa* from which the values given in the text were derived. This call was recorded at Dichard Creek, Glen Innes, (locality 13a), at a dry-bulb air temperature of 13.0°C.
B. An expanded waveform of the eighth doublet in the call depicted in A.
C. A waveform of the complete advertisement call of *Litoria citropa* from which the values given in the text were derived. This call was recorded at the Rocky River Road crossing on the Brodribb River, 17.5 km NNE of Orbost, Vic. at a wet-bulb air temperature of 17.5°C.



greater by up to 9 dB in pairs 1-7, and by 12 to 20 dB in pairs 8-13. Durations of doublets range from 291 to 372 ms (mean = 334); intervals between doublets range from 84 to 159 ms (mean = 118). The repetition rate of the doublets is 1.35 s^{-1}. The dominant or peak frequencies are within the range of 1360-1480 Hz, with means of 1405 Hz for the first notes and 1454 Hz for the second notes. There are 10-15 pulses (mean = 14.1) in the first notes of each of the first seven pairs, and 4-6 pulses (mean = 4.8) in the remainder; with 13-23 (mean = 16.1) in the second note of the first seven pairs, and 9-11 (mean = 10.3) in the remainder. Ranges of durations of first notes are 72-93 ms (mean = 85.9) for the first seven pairs, 43-69 ms (mean = 59.8) for the others and 126-149 ms (mean 137.6) and 134-159 ms (mean 144.2) respectively for the second notes. Pulse rates of first notes range from 125-167 p s^{-1} (mean 152.5) in the first seven pairs, to 46-85 p s^{-1} (mean 64.9) in the last six. For the second notes, the ranges for pulse rates are 92-182 p s^{-1} (mean 145.0) for the first seven pairs and 56-75 p s^{-1} (mean 64.9) for the last six.

Litoria citropa

The advertisement call of this species was described by Littlejohn *et al.* (1972) from the audiospectrographic and oscillographic analysis of two calls of one individual recorded (Nagra IIIB recorder, Electro-Voice EV 644 microphone) at Tonghi Creek 9 km W of Cann River Vic. (149° 05' E, 37° 34' S) on 24.x.1969. The male was calling on the bank at a wet-bulb air temperature of 10.5°C. Owing to background noise levels in the recording, only a tracing of a waveform was provided.

This relatively long call (3.2-3.6 s) was described as of complex temporal structure (i.e., strongly diphasic), with a long introductory note (910-920 ms) of high and regular pulse rate (46 p s^{-1}), followed by a sequence of irregularly produced pulses in groups of 5-7. The groups have durations between 80 and 120 ms and pulse rates of 34-57 p s^{-1} near the start, and are longer (245-500 ms) and of lower pulse rate (10-21 s^{-1}) near the end. The dominant frequencies range from 1350 to 1800 Hz within a broad band of frequencies between 1250 to 3600 Hz.

To confirm this description, and to provide an indication of possible effects of temperature, the last clear call in the recorded sequence of another individual of *L. citropa* was analysed. The recording was made at the Rocky River Road crossing on the Brodribb River 17.5 km NNE of Orbost Vic. (148° 33' E, 37° 30' S) by M. J. Littlejohn on 28.xi.1981. This frog was calling from vegetation at a height of about 50 cm, adjacent to the river, at a wet-bulb air temperature of 17.5°C. A wave form of this call is presented in Fig. 3C.

The call, which has an overall duration of 2.866 s, consists of a distinct first note which is a regular pulse train with a duration of 814 ms, a pulse rate of 187 p s^{-1} and a dominant frequency of 1640 Hz. A single pulse (duration approximately 7.0 ms) with a dominant frequency of 1600 Hz follows. The remainder of the call consists of eleven groups of 3-5 pulses but four pulses and one pair of pulses cannot realistically be grouped to allow calculation of a pulse rate; otherwise, pulse rates range from 31 to 84 p s^{-1}. The dominant frequencies of these pulses range from 1200 to 1300 Hz and the durations of the pulses range from 8.6 to 12.9 ms. The variable pulsatile second part of this call has a maximum amplitude about 5 dB higher than that of the introductory note.

Oviposition

Litoria subglandulosa

The advertisement call of the male was heard in the bag before amplexus occurred. Details of egg masses laid are presented in Table 2. Oviposition was not observed, but for each of the three captive pairs studied, a single egg mass was found adhering to the side of the bag, just below water level. The eggs were laid in a small, compact clump of two to three layers of extremely sticky, cohering capsules. Egg complements for two females were 292 and 425.

Another eight egg masses of this species were found at locality 8 on 4.xi.1994 by A. White and S. Gow. Each mass was attached to an overhanging leaf, a twig or a rock face in vertical or near vertical orientation, just below the water surface in a slowly flowing section of a pool (some in mid-stream). The pool was heavily shaded by an almost complete canopy cover. Steady rain had fallen three days earlier and the surface water temperature at 1400 h was 9.4°C. One of these masses, removed from the stream on a leaf and photographed, is shown in Fig. 2.

Litoria citropa

On 25.xi.1973, oviposition occurred after the male and female had been collected at Ourimbah Creek, NSW (locality 16, Table 3), at 2200 h. The frogs were placed in a plastic bag. The male soon began to call and the pair was in amplexus three hours after capture. At 0156 h on 26.xi.1973, the initial two sequences of oviposition activity occurred; at 0157 h, a further four oviposition sequences followed, with only about three seconds between each. Oviposition was complete by 0159 h.

In a typical sequence, the female dorsiflexed her body with outstretched hind limbs and produced a batch of eggs. The male fertilised them while cupping his feet in a fanning motion around the eggs. The female then scattered the eggs with three sudden kicking movements of her hind limbs. The eggs sank and spread in a single layer across the bottom. She

TABLE 4. *Comparison of embryos of* Litoria subglandulosa *and* Litoria citropa. Developmental stages are those of Gosner (1960)

Stage	Sample *L.subgland.* n	Sample *L.citropa* n	Mean embryo diameter/length (mm) *L. subgland.*	Mean embryo diameter/length (mm) *L. citropa*	Mean capsule diameter (mm) *L. subgland.*	Mean capsule diameter (mm) *L. citropa*	Description *L. subglandulosa*	Description *L. citropa*
2	4	4	1.59	1.73	3.57	6.10	*Animal pole:* black/ *vegetal pole:* dark grey	dark brown/ creamy white
17	9	15	2.17	3.12	-		*Body:* dark grey, yolk sac light grey *Head* (lateral view): acutely angled *Optic vesicle:* small, distinct bulge	dark brown/ creamy white acutely angled larger, indistinct bulge
21-22	3	9	6.53	6.76	-		*Gills:* anterior 3-4 branches posterior 4-5 branches	1-2 branches 2-4 branches (shorter)
24-25	1	8	7.39	9.65			*Lateral lines:* pigmented *Mouth-parts:* no tooth rows or keratinised jaw sheath	non-pigmented tooth rows, keratinised jaw sheath
							Hatching time: 6-10 days	4-6 days

then swam to another site and the process was repeated. During the final sequence, the female remained in the dorsiflexed position about three seconds longer, but produced no eggs. The male then released the female at the point when she began kicking her hind limbs.

The egg complement was 655. Embryos hatched in four - five days at water temperatures of 17°-23°C. Two other egg masses laid in captivity contained 890 eggs and 928 eggs and took four - six days to complete hatching at 16°-23°C (see Tables 3 & 4).

In the field, the eggs were found scattered over the substrate in shallow pools or slowly flowing sections of the stream, which is similar to the mode of deposition of eggs observed in captive pairs.

TABLE 5. *Dimensions of preserved embryos of* Litoria subglandulosa (mean in mm, range in parenthesis, stage - Gosner, 1960)

Stage	Sample	Embryo diam.	Capsule diam.
2	4	1.59 (1.56-1.64)	3.57 (3.12-4.51)
7-8	5	1.56 (1.56-1.56)	3.56 (3.36-3.85)
16	5	2.05 (2.05-2.05)	3.39 (3.28-3.53)
17	9	2.17 (2.13-2.34)	
20	6	5.80 (5.49-6.23)	
21-22	3	6.53 (6.48-6.64)	
23	2	6.80, 7.34	
24	1	7.39	

Embryonic development
Litoria subglandulosa

Mortality rates of embryos maintained in captivity were high. The survival rate (after removal from the stream), was greatest amongst embryos in the top layer of each mass. Those below this layer mostly ceased developing beyond about stages 8-12. Embryos from the egg mass held at locality 10 in water temperatures of 14°-21°C, survived the longest; hatching occurred from days 8 - 10 and only 17 reached stages 20 - 25. The mass from locality 3 did not develop beyond stage 18. Initially, the embryos from locality 4b continued to develop during the two days of immersion in the stream before higher temperatures away from the stream were experienced. Hatching occurred at stages 20 - 21 from days 6-8, with only eight embryos surviving. Embryos from the southern localities match the following description of those from the type locality 10.

Embryos laid early on 1.i.1974 (locality 10) were at stage 2 when a sample was preserved at 0945 h. The animal pole is black and the vegetal pole dark grey. There are two layers of jelly surrounding the perivitelline membrane. Measurements of embryos are given in Table 5. The embryos were at stages 7-8 after 8 h, and 8-9, after 12 h. Six embryos at stages 7-8, measured after preservation, have a smaller mean diameter than the same embryos measured live (1.7 mm live, 1.5 mm preserved; capsule diameter 3.6 mm live, 3.3 mm preserved). After 23 h, embryos were at stages 10-11, and after 38 h, at stages 12-13.

Stage 17 was reached after 62 h. A specimen drawn at stage 17 (Fig. 4A), is described:- prominent optic vesicle, pronephric swelling, slight anal bulge, large

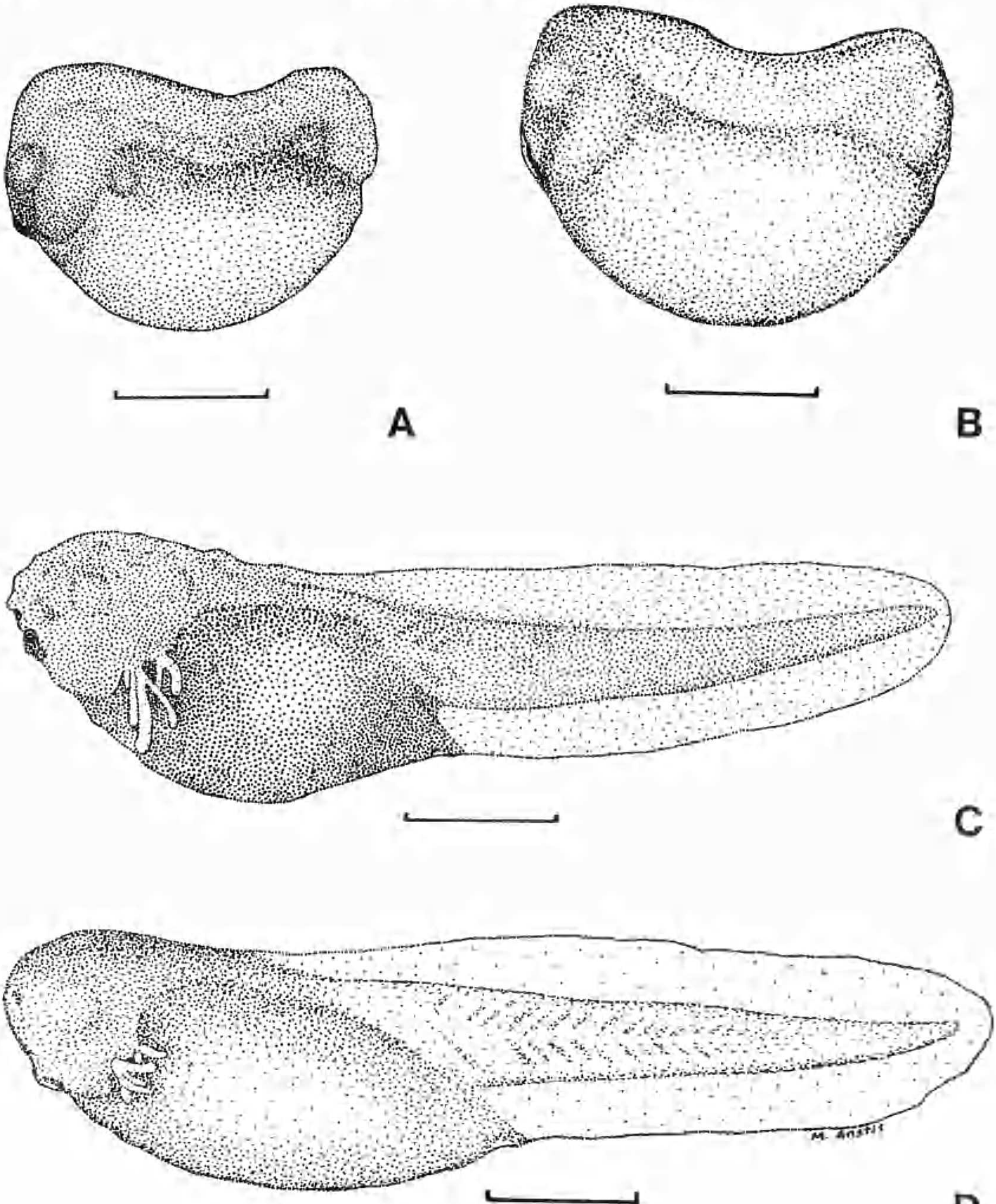


Fig. 4. Embryos of *Litoria subglandulosa* and *L. citropa*.
A. *L. subglandulosa* removed from its capsule, at stage 17.
B. *L. citropa* removed from its capsule, at stage 17.
C. *L. subglandulosa* just hatched, at approximately stage 21.
D. *L. citropa* just hatched, at approximately stage 21.
Scale bar = 1 mm. Stages are from Gosner (1960).

gill-plate swelling, with beginnings of muscular ridges along dorsal surface just below neural tube. U-shaped adhesive organ, slight stomodaeal groove beginning to form. Head truncate, acutely angled in lateral view. Tail bud short, rounded, with strong depression on each side below neural tube. Yolk sac grey, rest of body very dark grey. After some years in preservation, body appears dark and yolk sac lighter brown.

Embryos examined at 71 h were in stages 17-18:- growing tail bud pointing acutely to the left side of the body within firm jelly capsule: two visceral arches forming, narial pits beginning to develop.

After 95 h, stage 18:- optic vesicle more defined with groove forming between this and gill plate; neural tube, dorsal muscular ridges, narial pits and divided adhesive organs all more developed.

After 131 h, stages 19-20:- small external gills, gill circulation not apparent; head small, more rounded over cranial region, adhesive organs diminishing; optic vesicle depressed slightly in centre: live embryos dark grey dorsally, lighter grey over yolk sac, moving actively within capsule.

Hatching began eight days after oviposition; all surviving embryos had hatched after ten days. Embryos hatching first on day 8 were at stage 20 (in relation to optic development, but no gill circulation):- Optic vesicles indistinct, yolk sac large, deepened stomodaeal pit with adhesive organs close together at anterior end, a divided ridge at posterior end; gills developing, noticeably more advanced on sinistral side; vent tube not well differentiated: tail fins dusky grey, slightly arched dorsally; body dark grey brown in preservative, head region slightly darker.

Stage 21 was reached on day 10, in relation to gill development and lack of tail fin circulation only, (Fig. 4C):- two pairs of well-developed functional external gills, comprising 2-4 branches on anterior pair, 1-5 on posterior pair; adhesive organs small, translucent; optic vesicle undefined; fins translucent, deepening further, circulation not apparent; tail musculature poorly developed.

Five final hatchlings at 1900 h on day 10 were at stage 22 in relation to tail circulation, but other development was associated with stages 20-21:- cornea still not transparent, prominent but only partially pigmented optic vesicle, tail fins deepening; gills at maximum development, fully functional, longer in some specimens than others; adhesive organs merging to form small ridge; mouth triangular; line of pigment from tip of snout through each narial pit to eye.

Stage 23:- cornea transparent, eyes well developed, heavily pigmented; anterior half of body becoming transparent around nares; gills diminishing, operculum developing.

Stage 24:- vent tube more discernible, oral disc developing, with small triangular funnel above large oval depression to become lower labium.

By day 13, most remaining embryos were at early stage 25:- golden iridophores scattered in spots over dorsum, eyes black with scattered golden iridophores, patches of melanin over dorsal surface of tail musculature; tail fins, body wall mostly clear, with some dusky pigment present. Internarial region noticeably delineated with pigment, lateral line organs becoming visible.

By day 17, the development of the mouth was almost complete with the exception of the fine black filaments, which were either not yet present, or only short unpigmented roots. Dorsal surface further pigmented with more golden iridophores over areas pigmented with melanin, including iris; tail musculature pigmented dorsally, in well-spaced broad bands; flecks of pigment found over fins in older larvae, as yet not obvious; ventral surface clear, except for broad perimeter of iridophores.

Litoria citropa

Embryonic development was described by Tyler & Anstis (1975). A comparative summary of embryos of *L. citropa* and *L. subglandulosa* during stages 2, 17, 21 and 25 is given in Table 4. Figures 4B, D show stages 17 and 21. In general, *L. citropa* is larger than *L. subglandulosa* throughout embryonic development, with adhesive organs more prominent and gills smaller and less numerous at stage 21. At stage 25 and beyond, the lateral line organs remain unpigmented and mouthparts possess tooth rows and a keratinised jaw sheath (Fig. 4, Tyler & Anstis 1975). Otherwise, the two species have distinctly truncate, angular heads in stage 17 and similar body/tail shape throughout embryonic and larval development.

Larval behaviour

Litoria subglandulosa

Tadpoles of this species, observed at all localities in Table 1, were mostly found on the substrate in shallow, slowly-flowing sections of the stream on sand, amongst rocks or leaf litter. They were frequently found at the sides of the stream, swimming fast to deeper mid-stream or amongst rocks if disturbed. They were well camouflaged whilst on sand or grazing amongst rocks and appeared to feed on flocculent silt and algae. Tadpoles defaecated rapidly after capture and the abdominal region, while similar in width to the branchial region (or slightly less) in live specimens in the stream, was commonly narrower in preserved specimens.

Tadpoles observed adhering to the substrate rapidly pulled the body forward a distance of 2-3 mm by the use of the oral disc alone, in a rasping action. This process was repeated continually, resulting in a distinctive form of locomotion during feeding, which has not been described in other Australian suctorial species. Particles of a fine silt suspension were found amongst the dense, incurved papillae, buccal cavity and gut of recently-captured specimens.

The fine black filaments of the mouth were broken or missing in some specimens, or each was present only as a shorter white filament or core, without the black outer surface (or pigmentation).

Litoria citropa

The tadpoles were found in small rock pools (either associated with the main stream or segregated when river levels were lower), and in larger pools or slowly flowing sections of the stream. They were also found on the substrate, but unlike *L. subglandulosa*, were not observed moving forward by the use of the mouth alone; the tail and body were also involved. They appeared to feed on flocculent silt and most individuals examined live in the streams, had well-filled intestines (the abdominal region being as wide as, or wider than the branchial region). When disturbed they took cover under rocks or leaf litter. They were well camouflaged on the sandy floor and the dorsal colour varied from light to darker golden brown, depending on the colour of the substrate and light intensity.

Discussion

Population trends

Comparative field observations of the 1960s-70s and 1990s showed a marked decline in the population status of *L. subglandulosa* at the type locality, indicating a need for comprehensive studies on population trends of this species across its entire distribution.

Advertisement calls

The calls of *Litoria subglandulosa* and *L. citropa* differ markedly in structure (Fig. 3A, C) and cannot be of any assistance in the confirmation of relationships based on other criteria. As noted by Watson *et al.* (1991), the audiospectrograms of the advertisement calls of *L. citropa* and *L. spenceri* are of similar diphasic structure; they differ, however, in that the following notes in the call of *L. spenceri* are more regularly pulsed and of higher pulse rate.

Oviposition and embryos

From observations of oviposition sites of *Litoria verreauxii, L. dentata, L. phyllochroa, L. caerulea, L. chloris, L. freycineti, Limnodynastes peronii, Lim. tasmaniensis, Lim. ornatus* and other species of Australian frogs, it has been noted that each deposits eggs in a similar manner whether in the field or in captivity (Anstis 1976, Anstis, unpub.). Similarly, *L. citropa* scatter eggs over the substrate in both captive and field situations, and *L. subglandulosa* attach the entire egg mass to a surface just below water level. The egg mass of *L. subglandulosa* is adapted to the lotic environment, being compact in form and highly adherent.

Embryos of *L. subglandulosa* that survived beyond stages 8-12 were mainly from the outside layer of capsules. Mortality may be attributed to reduced oxygen levels associated with higher still – water temperatures in the laboratory of up to 24°C, compared with 9.4°-15°C in flowing streams. The embryos from the egg mass at locality 4b continued development during the initial two days of immersion in the stream but, after removal and placement in the laboratory, development gradually ceased over the next four days in the majority of cases.

The periods of 6-8 and 8-10 days taken by two egg masses to hatch (while maintained in containers) are slower than those of other known stream-dwelling hylids of lower altitudes, including *L. citropa* (Tyler & Anstis 1975; Anstis unpub.). Further comparisons can be made when data are available for developmental rates of egg masses within the stream.

The egg capsules of *L. citropa* are not as adherent as those of *L. subglandulosa*. As they are scattered over the bottom of still pools or very slowly flowing sections of the stream, stronger adhesive properties

TABLE 6. *Comparison of body proportions of larvae of* Litoria subglandulosa.
Type Locality 10 compared with new localities 2, 6a & 7a (Table 1).
(Measurements in mm; mean with range in brackets).
Stages 35 & 36 (Gosner 1960).

Morphometric Character	Type Locality 10 n = 8	Localities 2, 6a, 7a n = 8
TL	29.84 (26.40-35.00)	31.50 (28.50-33.75)
BL	12.19 (11.64-12.63)	11.88 (10.82-13.13)
BW	7.42 (6.15-8.04)	7.64 (7.05-8.45)
BD	6.17 (5.74-6.64)	6.10 (5.58-6.72)
TD	5.86 (5.17-6.48)	5.87 (5.42-6.40)
TM	2.01 (1.64-2.29)	2.35 (1.89-2.71)
IO	2.49 (2.13-2.87)	2.75 (2.46-3.29)
IN	1.88 (1.80-1.97)	1.94 (1.80-2.05)
EN	1.46 (1.15-1.64)	1.37 (1.15-1.64)
MW	4.55 (3.77-5.25)	4.48 (4.10-5.00)

would not be advantageous. The embryos developed faster and had a much lower rate of mortality than those of *L. subglandulosa*, possibly attributable to the individual capsules being scattered over a broad area, facilitating oxygenation.

Larvae

Whilst slight differences in body proportions were noted between some of the northern and southern tadpoles of *L. subglandulosa* (Table 6), only a small sample from each area was examined.

A sample of *L. subglandulosa* tadpoles was also very difficult to maintain in captivity at higher temperatures and a second sample maintained in aerated water with filtration fared no better. Lacking keratinised jaw sheaths, they could not eat foods such as boiled lettuce and commercial fish food. Introduction of silt and detrital sediments taken from the streams in their natural environment resulted in some feeding, although the tadpoles did not grow as well as those in the streams.

The distinctive locomotive behaviour of the tadpoles involving forward propulsion with the use of the oral disc alone, distinguishes them from the similar sympatric species *L. phyllochroa* and *L. lesueuri*, both of which employ some tail movement during locomotion associated with feeding. Gradwell (1975) states that the M3c muscle in *L. subglandulosa* tadpoles is inserted in both the upper and lower labia, resulting in both labia being "pulled caudad simultaneously", whereas "most other suctorial tadpoles move their upper and lower jaws toward each other during their scraping action". This could explain the mechanism behind the distinctive movement observed in live tadpoles in the stream. Gradwell also notes that this species has, for its size, "the longest and densest papillae of the buccal mucosa", and these "may act as a sieve to exclude suspended particles above a certain size".

Examination of gut contents and further observations of feeding mechanisms are required to determine the functional morphology of the unique mouthparts of this species.

Acknowledgments

We are grateful to the Australian Museum and the Museum of Victoria for access to and loan of specimens. The NSW National Parks & Wildlife Service is acknowledged for permission to refer to records of *Litoria subglandulosa*. John Courtney provided the tape recording of *L. subglandulosa* analysed. Arthur White provided Figure 4, and with Karen Thumm, Jacquie Recsei and the late Shane Gow, added valuable observations on *L. subglandulosa* to this study. David, Dulcie and Ron Anstis, John de Bavay and Roy Scott assisted with field work. Stephen Richards, Michael Mahony, John de Bavay, Fred Parker and Michael Tyler constructively reviewed the manuscript.

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